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Skeleton of the Giant Deer *Megaloceros giganteus giganteus* (Blumenbach, 1803) (Mammalia, Artiodactyla) from the Irtysh Region near Pavlodar

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Abstract—An almost complete skeleton of the giant deer *Megaloceros giganteus giganteus* (Blumenbach, 1803) from the Dzhambul locality on the Irtysh River (Pavlodar Region, Kazakhstan) is described. About 80% of bones are intact, including the skull with well-preserved antlers. At present, the skeleton is mounted in the Pavlodar Local History Regional Museum. Comparative analysis of giant deer skulls varying in age from the southeastern West Siberian Plain has revealed stable characters distinguishing Middle and Late Neopleistocene specimens. These characteristics are considered to be of subspecies rank, allowing the identification of *Megaloceros giganteus ruffi* Nehring and *Megaloceros giganteus giganteus* (Blumenbach.) Changes in absolute and relative dimensions of the dentition and facial skull length are most indicative with reference to evolution.

Keywords: *Megaloceros giganteus*, Giant deer, morphology, skeleton proportions, Late Pleistocene, Western Siberia

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INTRODUCTION

The giant deer is a typical member of mammal faunas of the Middle and Late Neopleistocene of the West Siberian Plain and Kazakhstan, which occurred in the Irtysh, Khazarian, and Mammoth faunas. According to recent radiocarbon dating, the giant deer of Russia survived up to the Holocene and became extinct in the southwestern West Siberian Plain and Urals about 7600 years ago (a skeleton from Kamyshlov (Galkino after Pavlowa, 1908); noncalibrated age is 6816 ± 35 KIA-5669) (Stuart et al., 2004). S.K. Vasil'ev proposed an even later (4–5 ka) existence of the giant deer in the Novosibirsk Region (Vasil'ev et al., 2011). Neopleistocene remains of the giant deer in the southeastern West Siberian Plain are rather abundant but nonuniformly distributed. The Irtysh Region near Pavlodar is particularly rich in giant deer remains; they occur here in almost all Late Neopleistocene mammal localities from Podpusk to Urlyutyub. Several skulls have been recorded in a locality of the Irtysh Fauna (Tobolsk Time) near the village of Grigor'evka (Shpansky, 2011). Previous publications provide data of antlers from the Mindel–Riss (?) of the vicinity of the villages of Chernoyarka, Krasnoyarka, and Urlyutyub situated north of Pavlodar on the Irtysh River, which were referred to as *Megaloceros giganteus ruffi* Nehring, 1892 (Gromova, 1932; Belyaeva, 1933, 1935; Shcheglova, 1958). The first detailed description of giant deer remains from the Irtysh Region near Pavlodar was reported by Kozhamkulova (1969). Later, I describes skulls and postcranial fossils of the giant deer from Grigor'evka and other localities of the southeastern West Siberian Plain (Shpansky, 2011). The extreme scarcity of skeletons or even skeleton fragments of the giant deer complicates the recognition of temporal and spatial morphological changes of this taxon. The finds of isolated bones and skulls prevent complex analysis of *Megaloceros giganteus* (Blumenbach, 1803) as a biological species and complicate identification to subspecies. In the former Soviet Union, two noncontemporaneous subspecies, Middle Neopleistocene *Megaloceros giganteus ruffi* and Late Neopleistocene *Megaloceros giganteus giganteus*, have been recognized (Shcheglova, 1958; Shpansky, 2011). Because of the absence of a complete skeleton of *M. g. ruffi*, it is only possible to identify it based on skulls and antlers.

The following abbreviations are used in the present study: (KKM) Kemerovo Regional Museum; (MP PGPI) Nature Museum of the Pavlodar State Pedagogical Institute, Pavlodar; (PIN) Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow; (POIKM) Pavlodar Local History Regional Museum; (PM TGU) Paleontological Museum of Tomsk State University; (VZN) Showrooms of the Kemerovo Region Affiliated Branch of the Regional

Fig. 1. Geographical position of the Dzhambul locality.

Information Stock of the Siberian Federal District (Novokuznetsk).

MATERIAL AND METHODS

The present study describes an almost complete skeleton of *M. g. giganteus* (specimen POIKM, no. KP 7191) found and excavated by S.A. Amrenov in 1978 on the right bank of the Irtysh River near the Dzhambul State Farm, 9 km northwest of the village of Lebyazh'e (presently Akku), Pavlodar Region, Kazakhstan (about 51°30′N, 77°40′E) (Fig. 1). It lay on the left side at a depth of 12 m in a layer of whitish gray carbonate clay, with a light blue tint and dark brown clayey interbeds. The total thickness of clays was estimated during excavation as approximately 2 m. This strata are correlated with shallow lacustrine deposits of Lake Aksor, which were formed in the first part of the Karginian Time. V.S. Zykin has provided a detailed description of the geological section of Late Neopleistocene lacustrine deposits located 1.5 km south of the village of Lebyazh'e (Zykin et al., 2002), which outcrop on the right bank of the Irtysh River and extend for 24 km from Lebyazh'e to Podpusk. The position of the skeleton is considered to correspond to layers 19–22, but with a somewhat greater thickness (Fig. 2). In

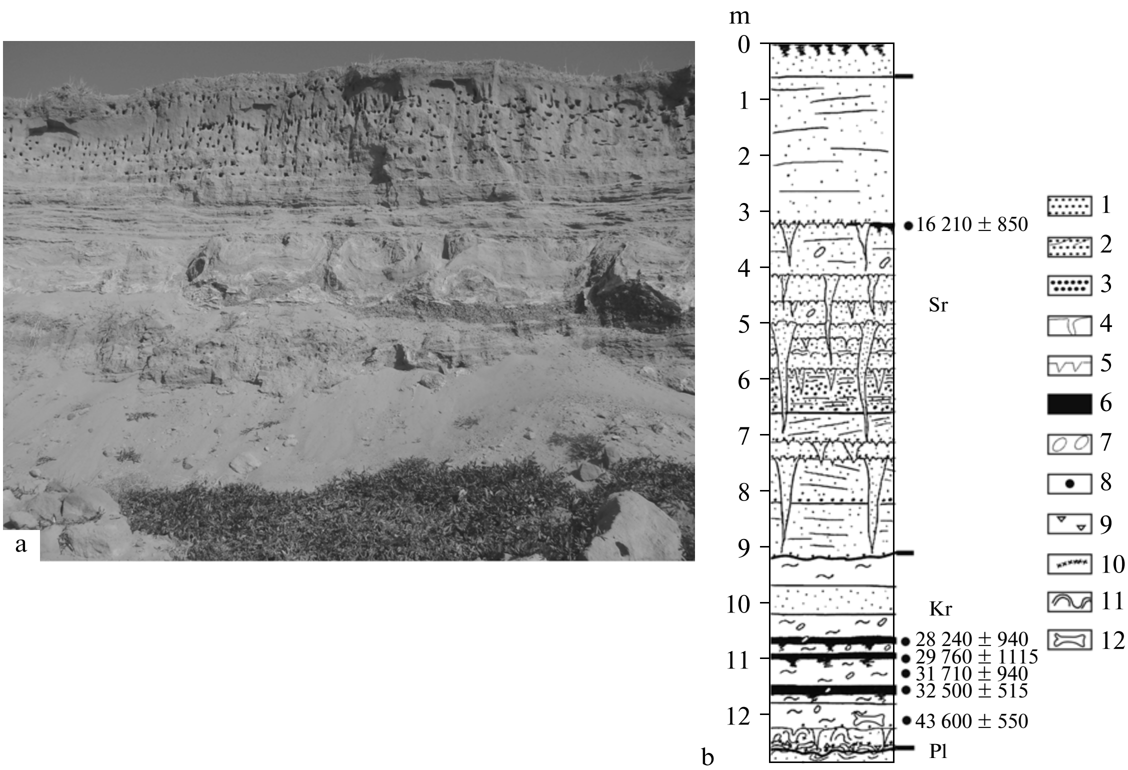


Fig. 2. Dzhambul locality: (a) general appearance of the outcrop (original photograph, 2008); (b) scheme of section of the Karginian–Sartanian beds of Lake Aksor outcropping on the right bank of the Irtysh River (after Zykin et al., 2002, supplemented). Designations: (*1*) sand, (*2*) bedded sand, (*3*) pebble, (*4*) primary sandy veins, (*5*) wedges of drying, (*6*) soil, (*7*) burrows of digging mammals, (*8*) radiocarbon dates, (*9*) weathered rock, (*10*) carbonate crust, (*11*) cryoturbation, (*12*) position of skeleton of *Megaloceros giganteus giganteus* (Blum.), (*Sr*) Sartanian strata, (*Kr*) Karginian strata, (*Pl*) Pliocene.

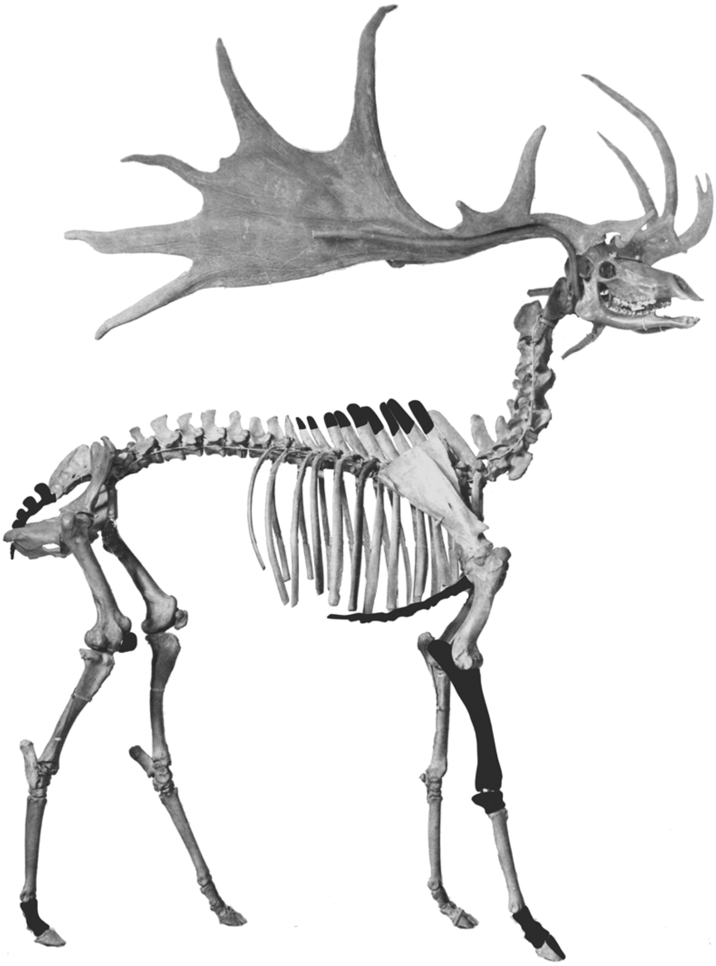


Fig. 3. Skeleton of *Megaloceros giganteus giganteus* Blum. from Dzhambul, specimen POIKM, no. KP 7191; Kazakhstan, Pavlodar Region, Dzhambul locality. Black color marks damaged and lost bones.

2010, using a rib fragment of the deer skeleton taken by the author, radiocarbon dating was performed: 43600 ± 550 (OxA-20250), with help of AMS analysis in the laboratory Oxford Radiocarbon Acceleration Unit (Great Britain).

A.N. Seleverstov restored damaged bones, produced molds of missing bones, and mounted the skeleton in the Pavlodar Local History Regional Museum in 1981 (Fig. 3). This skeleton has not yet been described.

Comparative material includes the following skulls and postcranial bones stored in the museums of southeastern Western Siberia:

MP PGPI: nos. 582, 1175, without no., skulls; no. 721, lower jaw; Grigor'evka locality, Pavlodar Region (Shpansky, 2011);

KKM: no. 51/129, skull; Komissarovo locality, Kemerovo Region (Shpansky, 2011);

VZN: without no., lower jaw; Kondoma River locality, Kemerovo Region (Shpansky, 2011);

PM TGU: no. 55/1, skull fragment; Grigor'evka locality, Pavlodar Region.

The proportions of the postcranial skeleton were compared with the previously described skeletons of specimen SM/9925 from Kamyshlov (Sverdlovsk Region) and specimen PIN, no. 337 from Sapozhok (Ryazan Region) (Pavlowa, 1908, 1929). 2

The deer skull from Dzhambul was compared with skulls from other localities of the southeastern West Siberian Plain based on the measurements and indices applied by Vislobokova (1990). Postcranial bones were measured using the technique developed by Gromova (1950); the indices of the width of cylindrical bones were calculated relative to the greatest length. In addition, published data on remains of the giant deer from the former Soviet Union and central Europe were used.

DESCRIPTION AND COMPARISON

More than 80% of skeleton bones are preserved; most of the lost bones belong to the right body side, probably because the deer skeleton from Dzhambul was buried lying on the left side; in particular, the right radius and ulna, right carpals, right patella, and caudal vertebrae are absent. The neural spines of nine anterior thoracic vertebrae and lower ends of some ribs are damaged to varying extent; the sternum is represented by two fragments, although they are not mounted in the skeleton; the wing of the left ilium is damaged. The phalanges on the right and left limbs are differently preserved; on the right side, only the third phalanges of the fourth anterior digit and third hind digit are preserved; on the left side, both first phalanges of the hind limb, both second phalanges of the forelimb, and the third digit of the hind limb, the third phalanx of the fourth digit of the forelimb, and the third digit of the hind limb are preserved (Fig. 3). All bones are light brown.

The skull is well preserved (Pl. 14, fig. 1; Table 1), only the nasals are absent; the premaxillae are slightly damaged. The frontal and parietal sutures are completely obliterated. The skull has a pair of antlers, suggesting that the animal died at the end of autumn or at the beginning of winter. The antler span is at least 3.5 m; this measurement is approximate because of certain displacement of antlers from the initial position. The distance between the antler bases is 78 mm (in *M. giganteus ruffi* from Western Siberia, it is 75–92 mm). The dental row of P^2–M^3 is 142 mm long (150 mm in the skull without no. from Grigor'evka; 30–30.5% of the basal skull length), that is, the mean value for *M. giganteus* from Eastern Europe (133–156 mm) and somewhat less than in West European deer (150–153.3 mm) (Shcheglova, 1958; Croitor et al., 2006). It is noteworthy that the absolute and relative lengths of the upper dental row of *M. g. ruffi* from Grigor'evka and Komissarovo are much greater, 174–178 mm (32.8–34.9% of the basal skull length) (Shpansky, 2011). The teeth of the giant deer from Dzhambul are (P^2) 21.5 mm, (P^3) 22 mm, (P^4) 21 mm; (M^1) 28.4 mm, (M^2) 30.5 mm, (M^3) 30 mm of length; the M^1–M^3 row is 88 mm long; and the P^2–P^4 row is 63 mm long. It is impossible to measure the width of individual teeth, because the jaws are closed in the mounted skeleton. The greatest distance between the upper dental rows on the buccal surface at M^2 is 165 mm wide.

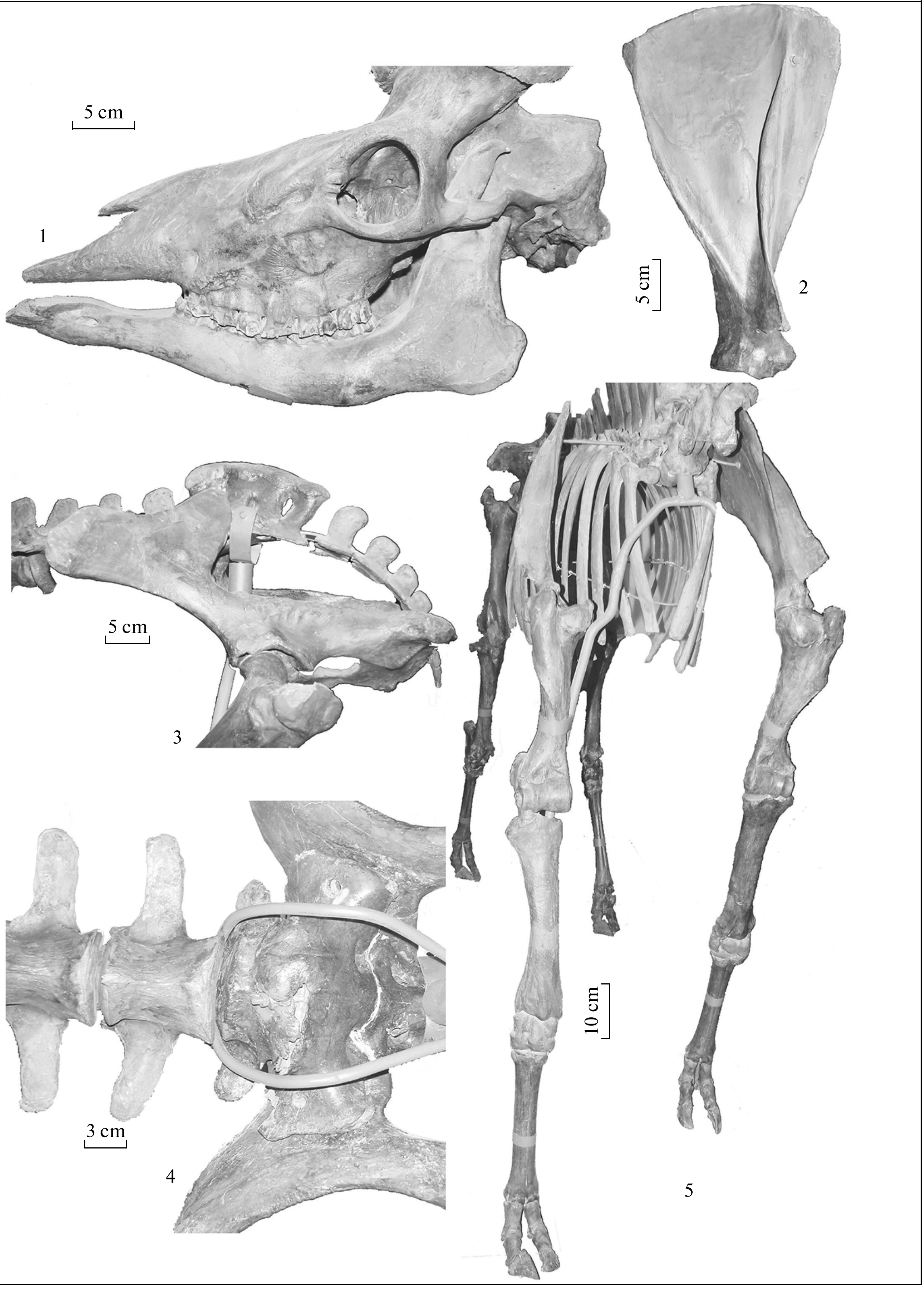
Comparative analysis involves skulls of the giant deer from noncontemporaneous localities of the southeastern West Siberian Plain. The Grigor'evka locality (Pavlodar Region) has yielded three skulls and one skull fragment of the giant deer from two noncontemporaneous bone horizons; they differ in preservation and accompanying fauna (Irtysh and Mammoth faunal assemblages: Shpansky, 2011) (Table 1). Two skulls from the lower bone level of this locality (specimens MP PGPI, nos. 582 and 1175) dated Middle Neopleistocene (Tobolsk Horizon) and the skull from Komissarovo (specimen KKM, no. 51/129) are referred by us to *M. g. ruffi* and skulls (specimens MP PGPI without no. and PM TGU, no. 55/1) from the upper bone level of Grigor'evka (Late Neopleistocene, Karginian Horizon) and skull of the skeleton from Dzhambul are rather similar to skulls of East European deer referred to as *M. g. giganteus.* Previously, Shcheglova (1950, 1958) attempted to divide the giant deer into two noncontemporaneous subspecies, Middle Neopleistocene *M. g. ruffi* and Late Neopleistocene *M. g. giganteus*, based on antler morphology. In addition to differences in size and antler shape, available material shows certain distinctions in characteristic skull measurements.

Figure 4a shows the diagrams of skull indices of *Megaloceros giganteus* of the southeastern West Siberian Plain. The curves displayed are very similar to that of skulls from the Irtysh Region near Pavlodar and Komissarovo (Kuznetsk Basin) and some differences were reported by Vislobokova (1990) without information on the origin of the material. According to Vislobokova, the frontal length index (character 9a) and cerebral–facial ratio (index 3) are significantly lower. The general similarity between index curves for skulls from the Irtysh Region near Pavlodar concerns both subspecies, *M. g. giganteus* and *M. g. ruffi*. Therefore, to show the differences more prominently, the curves including the most distinctive skull measurements of these subspecies from West Siberian localities are provided (Fig. 4b). These distinctive measurements include characters 1, 6, 7, 12, 16, 17, 19, 21, 22, and 26 and indices 2, 4, 12a, 16, 17a, 18a, 19a, 20a (Table 1), which reflect two important characteristics, the elongation of the facial region and reduction of the dental row length in Late Neopleistocene *M. g. giganteus* compared to Middle Neopleistocene *M. g. ruffi* (Shpansky, 2011).

In *M. g. giganteus*, the skull length (measurement 1) and internal distance between the antler bases (measurement 22) are smaller than in *M. g. ruffi.* A decrease in the dental row length (measurement 19) in West Siberian deer is accompanied by an increase in the diastema length (measurement 17); in *M. g. giganteus*, it is greater (160–170 mm) than in *M. g. ruffi* (127–139 mm). A decrease in the upper dental row length is caused by a decrease in the molar row length (M^1–M^3), so that the length ratio of premolars and molars increases from 60–64.8% in *M. g. ruffi* to 71.6–72.2% in *M. g. giganteus.* The elongation of the facial skull region in Late Neopleistocene deer is also manifested in relative elongation of the palate (indices 2, 17, and 20). Comparison of West Siberian giant deer with animals from Eastern and Western Europe is complicated because of a few available measurements and frequently different measurements reported in publications.

The deer from Dzhambul has large antlers; both have breaks of the bar at a small distance from the burr. The right antler is preserved to a somewhat lesser extent than the left counterpart; this is probably connected with the fact that the antler was for a long time on the day surface (since the corpse lay on the left side), suggesting that the burial formation took a

Plate 14



Explanation of Plate 14

Figs. 1–5. *Megaloceros giganteus giganteus* (Blumenbach, 1803), specimen POIKM, no. KP 7191; Kazakhstan, Pavlodar Region, Dzhambul locality; Upper Neopleistocene, Karginian Horizon: (1) skull, lateral view; (2) right scapula, lateral view; (3) pelvic region, lateral view; (4) pathological expansion of vertebrae in the lumbar–sacral region, ventral view; (5) general appearance of forelimb skeleton.

Table 1. Skull measurements of *Megaloceros giganteus* (Blum.) from the Irtysh Region near Pavlodar and Kuznetsk Basin

Measurements, mm	Komissa-rovo	Grigor'evka				Dzhambul
	KKM no. 51/129	MP PGPI no. 582	MP PGPI no. 1175	MP PGPI without no.	PM TGU no. 55/1	POIKM, no. KP 7191
Subspecies	*M. giganteus ruffi*			*M. giganteus giganteus*		
1. The basic length of a skull	530	510	518	C450 (500)	–	465
2. Length of anatomical braincase axis from basion to interorbitale		250	265	260	–	–
3. Length of anatomical axis of facial region from prosthion to interorbitale		320	330	C310 (335)	–	320
4. Greatest skull width at orbits	250	C250	270	C270	–	260
5. Greatest occipital width	198	210	200	200	–	210
6. Postorbital skull width	215	205	212	C190	–	200
7. Facial region width at constriction	101	84	84	90	84	84
8. Parietal length from occipital crest to frontal suture		116	136	130	–	130
9. Frontal length from frontal suture to nasals		190	200	190	–	200
10. Greatest occipital depth	130	120	150	127	–	120
11. Skull depth from sphenobasion to frontal suture		160	170	160	–	160
12. Facial region depth from interorbitale to posterior edge of dental row		118	120	132	–	~132
13. Height of bone opening in nasals		78	66	71	77	64
14. Length of bone opening of nasals		65?	110 (158)	C75(125)	C100	76
15. Distance from prosthion to the anterior point of orbit at lachrymal–zygomatic suture		255	295	C250 (275)	c250	295
16. Distance from basion to posterior point of orbit near frontal–zygomatic suture		215	230	205	–	200
17. Distance from P^2 alveolus to prosthion	132	127	139	C117 (170)	c135 (~160)	160
18. Distance from posterior edge of M^3 alveolus to prosthion	309	302	314	C260 (310)	c273	305
19. Dental row length	174	178	174	150	144	142
20. Distance from choana to prosthion	282	299	302	C250 (300)	c262	295
21. Postantler skull width	130	120	114	119	–	114.5
22. Distance between internal edges of antler bases	92	84?	75	68	–	78
23. Transverse (horizontal) diameter of antler base	77/82	69.5	73/78	73/76	–	91
24. Antler base length along internal edge		44	31	41	–	40
25. Height-to-width ratio of foramen magnum	40/34	45/37	43/41	42/40.5	–	/45
26. Width of occipital condyles	110	108	106.5	116	–	118
27. Greatest antler span	C1665	C1500	–	–	–	~3500
28. Greatest antler length along large curvature		?	–	–	–	1700
29. Antler length along straight line	C1040	C900	–	–	–	
30. Anteroposterior/transverse burr diameters	120/110	102/84	–	107/94	–	

Table 1. (Contd.)

Measurements, mm		Komissa-rovo	Grigor'evka				Dzhambul
		KKM no. 51/129	MP PGPI no. 582	MP PGPI no. 1175	MP PGPI without no.	PM TGU no. 55/1	POIKM, no. KP 7191
Subspecies		*M. giganteus ruffi*			*M. giganteus giganteus*		
Indices, %	Vislobokova, 1990						
1. Braincase length (2) : (1)	44.0		49.0	51.2	52.0		
2. Facial region length (3) : (1)	67.0		62.7	63.7	67.0		68.8
3. Ratio of braincase to facial region (2) : (3)	66.0		78.1	80.3	77.6		
4. Greatest skull width (4) : (1)		47.2	49.0	52.1	54.0		55.9
5a. Occipital width (5) : (1)	36.0	37.4	41.2	38.6	40.0		45.2
6a. Postorbital width (6) : (1)	43.0	40.6	40.2	40.9	>38.0		43.0
7. Snout width at narrowing (7) : (1)		19.1	16.5	16.2	18.0		18.1
8a. Parietal length (8) : (1)	27.0		22.7	26.3	26.0		28.0
9a. Frontal length (9) : (1)	29.0		37.3	38.6	38.0		43.0
10a. Occipital depth (10) : (1)	25.0	24.5	23.5	29.0	25.4		25.8
11a. Skull depth at bregma (11) : (1)	33.0		31.4	32.8	32.0		34.4
12a. Facial region height at interorbitale (12) : (1)	29.0		23.1	23.2	26.4		~28.4
13a. Height of bone opening of nasals (13) : (1)	14.0		15.3	12.7	14.2		13.8
14a. Length bone opening of nasals (14) : (1)	25.0		12.7?	21.2	25.0		16.3
15. Bone opening of nasals (13) : (14)			120?	60.0	56.8		84.2
16. Orbit position (15) : (16)	130.0		120.0	128.0	134.0		147.5
17a. Elongation of facial region (17) : (1)	29.0	24.9	24.9	26.8	34.0		34.4
18a. Position of posterior edge of dental rows (18) : (1)	60.0	58.3	59.2	60.6	62.0		65.6
19a. Dental row length (19) : (1)	32.0	32.8	34.9	33.6	30.0		30.5
20a. Palatal length (20) : (1)	60.0	53.2	58.6	58.3	60.0		63.4

rather long time. The antler palmation is well developed, triangular; the palmation plane is positioned at an angle of about 180° to the beam axis; the tines are long and located on the anterior margin; the posterior side has one tine at the palmation base. The antlers are almost symmetrical; the left one is slightly larger; its greatest length from the burr to tip of the farthest process is 170 cm; the greatest width of the palmation is 53 cm. The bar circumference at the burr is 23.5 cm; the circumference of the antler base is 25.8 cm. The supraorbital tines are very large, wide in the middle part, with a long, internally curving end.

In the deer from Dzhambul, both lower jaw rami are well preserved. The distance between the horizontal rami at the angular process (greatest) is 185 mm long. The lower jaw has a thickened, but low horizontal ramus; in the area of the diastema, the length is the greatest among giant deer from the southeastern West Siberian Plain (Table 2). Incisors are absent; all other teeth are well preserved and moderately worn. The incisor margin is 59 mm wide. The dental row is somewhat shorter than in deer from Krasnyi Yar (Tomsk Region). The length of M_3 is small, which is particularly appreciable against a background of the signifi-

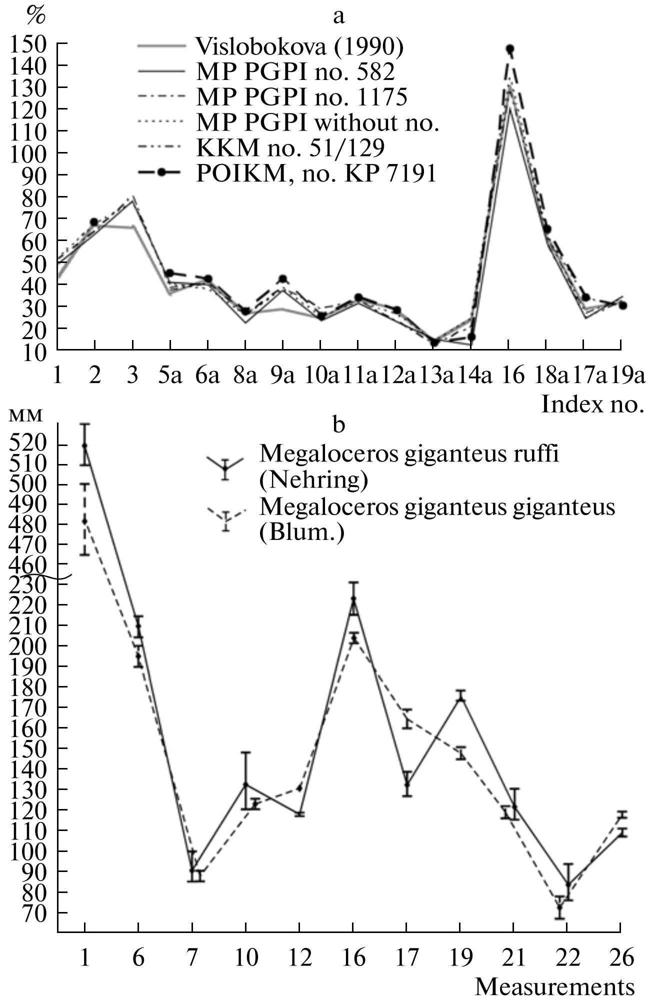


Fig. 4. Comparison of skulls of the giant deer *Megaloceros giganteus* (Blum.) of the southeastern West Siberian Plain: (a) indices for individual specimens (method after Vislobokova, 1990); (b) measurements (generalized for subspecies), connecting lines are drawn through mean values; the numbers of indices and measurements correspond to Table 1.

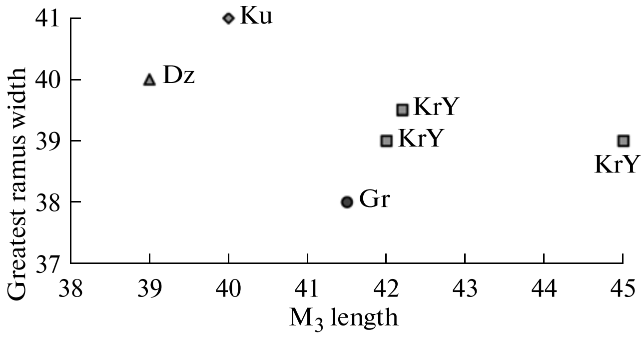


Fig. 5. Greatest width of the horizontal ramus of the lower jaw combined with the M_3 length in *Megaloceros giganteus* (Blum.). Designations: (*Dz*) Dzhambul (Pavlodar Region); (*Gr*) Grigor'evka (Pavlodar Region); (*KrY*) Krasnyi Yar (Tomsk Region); (*Ku*) Kuznetsk Basin.

cantly thickened horizontal ramus (Fig. 5). The lower jaws from Ilford (Lister, 1994) show similar proportions. The coronoid process of the ascending ramus is straight, with a sharp hook at the end.

The vertebral column (Pl. 15, figs. 1, 2) of the deer from Dzhambul is preserved almost entirely, except for caudal vertebrae. The neck consists of seven vertebrae 76 cm of total length (Pl. 15, figs. 1a, 1b). The vertebrae are massive; the atlas is 9.1 cm high, 22 cm wide at the wings; the anterior and posterior facets are 11.5 and 12 cm wide, respectively; and the spinal foramen is 5.3 cm wide and high posteriorly. The upper process of the epistropheus is relatively low, gently descending along a straight line to the anterior margin; posteriorly, the process is 4 cm high. The upper process of the third vertebra is absent; only a small, short, and sharp crest is preserved. The anterior lower processes are hooked internally. The neural spines of succeeding cervical vertebrae gradually increase in length. In the fourth vertebra, it is short, with a knobbly thickening at the end; in the fifth vertebra, it is inclined slightly anteriorly. The neural spine of the sixth vertebra is inclined anteriorly rather strongly and overhangs the preceding vertebra. The neural spine of the 12-cm-long seventh vertebra is directed strictly upwards, but the position of its centrum relative to the preceding vertebra changes considerably, since between the sixth and seventh vertebrae, the neck curves abruptly upwards. The posterior part of the centrum of the seventh vertebra has facets for the first pair of ribs.

The vertebral column (including the thoracic and lumbar vertebrae) is 133 cm long. The total length of 13 thoracic vertebrae is 86.5 cm; six lumbar vertebrae are 46 cm long. It is interesting that, for the skeleton from Kamyshlov (Galkino) of the Sverdlovsk Region (specimen no. SM/9925), Pavlowa (1908) reported somewhat different data on the regions of the vertebral column, i.e., six cervical vertebrae, ten thoracic (beginning from the third, while two anterior vertebrae are absent), and eight lumbar vertebrae; the caudal vertebrae are also absent. The centra of the thoracic vertebrae are positioned at approximately the same level and the dorsum outline is determined by the length and direction of neural spines. The giant deer lacks a hump-shaped bend of the dorsum, in contrast to that of bison (*Bison priscus*). The neural spines of the first nine thoracic vertebrae of the skeleton from Dzhambul are damaged in the upper part. This is probably bites, since all vertebrae are disrupted at almost the same height (at present, the spines are restored and it is difficult to establish the true cause). The longest spine is in the second vertebra; on the internal side, it is 38 cm long. In succeeding thoracic vertebrae, the neural spines gradually decrease in length towards the lumbar region. In the deer from Kamyshlov, the longest spine is in the fifth vertebra; it is 35 cm long (Pavlowa, 1908). In first eight thoracic vertebrae of the deer from Dzhambul, the neural spines are inclined posteriorly at approximately the same angle and parallel to each other. The neural spines are rectangular, without a bulge or curvature. In the 9–12th vertebrae, the neural spines are inclined posteriorly to a greater extent and curve slightly caudally, so that the dorsum apparently curved slightly downwards. At this curvature, the skeleton is 159 cm high. The lumbar vertebrae are similar in size to the posterior thoracic vertebrae; they (vertebral centra) only gradually increase in width. The neural spines of all lumbar vertebrae remain almost constant in height (Pl. 15, fig. 2a). The last lumbar vertebra is almost completely fused with the sacrum due to pathological expansion of its caudal part.

The rib cage consists of 13 rib pairs, which curve only slightly; therefore, it is plausible that it was flattened in the sagittal plane. The first rib pair gradually expands towards the lower end, with the greatest width of 45 mm. The sixth and seventh ribs are the longest, 53 cm long each.

The sacrum consists of four fused vertebrae. Ventrally, the total sacrum length is 21 cm along a straight line; the wings are 20.5 cm wide. On the ventral side, the anterior end of the sacrum has a pathological expansion. The centrum of the first sacral vertebra has a hooked projection, which almost completely covers from below the last lumbar vertebra (Pl. 14, fig. 4).

The scapulae are generally well preserved, but have small cracks. These bones are triangular, with an even upper margin, which is 270 mm wide. The glenoid cavity is almost round in outline; it is 73.6 mm long and 69.5 mm in diameter. The scapula is 465 mm long along the axis and 69.5 mm wide at the neck.

Both humeri are preserved; they are relatively short, only 355 mm long, but rather massive. The diaphysis is 48.8 mm wide (49 mm in the left bone); the proximal epiphysis is 123 mm (121.7 mm) wide and 129.5 mm (131 mm) in diameter; the distal epiphysis is 96.6 mm (97 mm) wide; the trochlea is 86.5 mm (88 mm) wide and 93 mm (92 mm) in medial diameter and 69.5 mm (68.4 mm) in lateral diameter.

The preserved left radius is relatively massive, has sharply outlined and distinctly projecting longitudinal crests on the anterior side of the distal end. The crests are parallel to each other and their lower ends are displaced medially, in contrast to the crests on the radii of elks, which are less pronounced and diverging. The proximal epiphysis of the radius has a distinct lateral epicondyle in the shape of a projection. This projection distinguishes the radius of *M. giganteus* from that of *Alces alces* L. (the lateral margin of the facet sharply breaks), which frequently co-occur in the same localities. The bone is 380 mm long, its diaphysis is 53.8 mm wide; the proximal epiphysis is 103 mm wide and 54.4 mm in diameter; the distal epiphysis is 88.4 mm wide and 62.7 mm in diameter.

Of the carpals, only two (left) bones are preserved, i.e., the cuneiform and trapezoid. The cuneiform is 54.1 mm in anteroposterior diameter, 26.7 mm wide, and 40 mm high. The trapezoid is 44 mm in anteroposterior diameter, 36 mm wide, and 28 mm high.

The metacarpals of the deer from Dzhambul are medium-sized for West Siberian deer (Shpansky, 2011). They are 335 mm long; the diaphysis is 44.9 mm wide (43 mm in the right counterpart); the proximal epiphysis is 73 mm wide and 51.4 mm in diameter; the distal epiphysis is 72.1 mm wide and 43.5 mm in diameter.

The pelvic bones are wide at the iliac wings and narrowed at the glenoid cavity and ischia. The makloks of iliac wings are turned widely laterally; the internal iliac tubercle extends posteriorly; as a result, the anterior margin of the maklok tubercle is at the level of the lateral process of the fifth lumbar vertebra. The iliac body extends anteriorly and upwards from the acetabulum. The acetabulum is round, widely open; the margins of the pelvic articular surface are turned externally. The ischia and obturator foramina are tuned in the horizontal plane; the dorsal margin of the ischiadic tubercle does not project above the ischiadic spine (Pl. 14, fig. 3). The pelvis length from the anterior margin of the maklok of the iliac wing to the posterior margin of the ischiadic tubercle is 500 mm. The maximum width at the iliac wings (at makloks, from below) is 458 mm; the minimum width at articulations with the sacrum is 120 mm; the minimum width between the lower margins of acetabulum is 200 mm (in the specimen from Kamyshlov, it is 210 mm wide: Pavlowa, 1908); the width at the projections of the ischia is 210 mm.

The left and right femora of the giant deer from Dzhambul are 450 and 460 mm long, respectively. The distal epiphysis is 123 mm wide and 150 mm in medial diameter; the diaphysis is 46 mm wide.

The patella is widely rhombic, with an extended lateral corner in the shape of an inflated petal. Its lower part is wide, with a slightly projecting lower margin of the longitudinal crest. The upper bone edge is round; the longitudinal crest in the mounted position in the hind limb is positioned vertically. The bone is 85 mm long and 70 mm wide.

The tibia of the deer from Dzhambul are much larger than that of the giant deer from Krasnyi Yar (420 mm long: Shpansky, 2011) and from Kamyshlov (350 mm long: Pavlowa, 1908); it is 470 mm long and 51.3 mm wide at the diaphysis. Despite a large size, the bone looks slender (the proximal epiphysis is 125 mm wide and 121 mm in diameter); the distal bone end is particularly graceful (the distal epiphysis is 85 mm wide and 61 mm in diameter); its relative width is considerably inferior to that of the specimen from Kamyshlov (Tables 5).

The metatarsal length of the giant deer from Dzhambul is similar to that of specimens from the

Table 2. Lower jaw measurements of *Megaloceros giganteus* (Blum.) from Western Siberia

Measurements, mm	Krasnyi Yar (Tomsk Region) $n = 5$ (Shpansky, 2011)	Kondoma River (Kemerovo Region) VZN without no.	Dzhambul, POIKM, no. KP 7191	Grigor'evka, MP PGPI, no. 721
Length: horizontal ramus	–	C180	400	394
dental row P_2–M_3	161		158	159
molar row	98?–100	101	98	
premolar row	62		66	61
at diastema	–		125	112
Width: articular process	–		44.5 sin; 45.0 dex	
horizontal ramus (greatest)	39–39.5	41	40	38
Height: anterior to P_2	40		41	44
posterior to M_3	61–63	53.5	57	62.5
at diastema (minimum)	–		28	26.7
anterior to articular process	–		135	
Length/width ratio: P_2	$\frac{17}{11}$		$\frac{16.5}{10}$	214
P_3	$\frac{22-22.5}{13-14}$		$\frac{22}{}$	$\frac{16}{9}$
P_4	$\frac{c20-24}{c16-16.3}$		$\frac{26}{}$	$\frac{21}{13}$
M_1	$\frac{c28}{20-21}$		$\frac{30}{}$	$\frac{24}{16.5}$
M_2	$\frac{32.7-34}{21.5-23}$	$\frac{26.5}{20}$	$\frac{30.5}{}$	–
M_3	$\frac{42-45}{19-22.8}$	$\frac{40}{23}$	$\frac{39}{}$	$\frac{41.5}{21.5}$

southeastern West Siberian Plain (Vasil'ev, 2005; Shpansky, 2011), but considerably greater than in the bones from Eastern Europe (Pavlowa, 1908; Svistun, 1968). The metatarsal proportions resemble the proportions of the tibia of the same specimen. They have a relatively narrow diaphysis, a very massive proximal epiphysis, and graceful distal epiphysis (Table 3).

Bones of the calcaneus joint are densely mounted and inaccessible for measuring.

The second phalanges of forelimbs are shorter than in the hind limbs, their proximal epiphysis is also absolutely smaller, while the distal epiphysis is more massive (Table 4). The ratio of the width of the proximal epiphysis of the second phalanges to its diameter in the forelimbs (79.9 and 90%) is much greater than in the hind limb (74.2%). This index is also much greater than that reported by Shcheglova (1958) for the giant deer from the Crimea (68.8–77.9%).

The third phalanges are approximately equal in size; in the forelimb, they are only slightly higher in connection with a larger size of the facet. The above differences between fore and hind phalanges show that the distal regions of the forelimbs are more massive as a result of a greater load on the forelegs.

SKELETON PROPORTIONS OF THE GIANT DEER

Structural features of the postcranial skeleton reflect adaptations of animals. Vislobokova (1990) believes that the proportions of skeleton regions, limb regions, extent of limb inclination relative to the ground, structural features of joints, the range of their flexion–extension movements, and the shape of ungulate phalanges are most informative. These characteristics reflect adaptive locomotor features. Feeding and

Table 3. Metatarsal measurements of *Megaloceros giganteus* (Blum.)

Measurements, mm Indices, %	Krasnyi Yar (Tomsk Region)		Krasnyi Yar (Novosibirsk Region) $n = 10$ (Vasil'ev, 2005)	Sapozhok (Ryazan Region) PIN, no. 337 (Svistun, 1968)	Kamyshlov (Sverdlovsk Region) SM, no. 9925 (Pavlowa, 1908)	Romankovo (Ukraine) $n = 3$ (Svistun, 1968)	Pavlodar Region	
	PM TGU $n = 5$ (Shpansky, 2011)	no. 2370 (Alekseeva, 1980)					Zhelezinka IZ, no. 49/P (Kozhamkulova, 1969)	Dzhambul POIKM, no. KP 7191
1. Bone length	371.5–391	c364	351–(369.6)–385	355	360	344–349		375
2. Diaphysis width in the middle	37–40	40	34–(37.3)–39.8	39	38.5	38.6–43.8	33	36.6; 37.6
3. Diaphysis diameter	34–44.6	45		50		44–46	43	
4. Proximal end width	56–64.6	63	54.5–(60.6)–68.4	65	64	60–61	50	64.8; 67.8
5. Proximal end diameter	59.5–65	c63	58.5–66.3	69			57	67.4; 68.8
6. Distal end width	74–75	72	70.1–(73.1)–78.8	76	70	69–78		70; 71.6
7. Distal end diameter	47–48	c46	42.3–48.3	51		44–46		44.8; 45.4
2 : 1	10.2–10.5		(10.1)	11	10.7	11–12.7		9.8; 10
4 : 1	16–17.4		(16.4)	18.3	17.8	17.4		18; 18.3
6 : 1	18.9–20.2		(19.8)	21.7	19.4	19.9–22.6		18.7; 19.1

Table 4. Phalanges measurements of *Megaloceros giganteus* (Blum.) from Western Siberia

Measurements, mm	Dzhambul (Pavlodar Region), POIKM, no. KP 7191		Krasnyi Yar (Tomsk Region), PM TGU (Shpansky, 2011)	Kamyshlov (Sverdlovsk Region) (Pavlowa, 1908)		Sapozhok, PIN, no. 337 (Svistun, 1968)
	anterior	posterior				
Phalanx 1 Length		77; 78.5	$n = 13$ 71–87.4	anterior 80	posterior 75	92
Diaphysis width		31.5; 32.5	25.1–34			32
Proximal epiphysis width		39.5; 40	31.6–38.2			39
Its diameter		52; 49	39.1–44			46
Distal epiphysis width		44	28–39			36
Its diameter		38.8	22–30			30
Phalanx 2 Length	55; 53.6	61	$n = 7$ 51.8–69	60	60	
Diaphysis width	28.5; 27	29	23–30			
Proximal epiphysis width	36; 34.6	35.4	31.8–40			
Its diameter	40; 43.3	47.7	29–47			
Distal epiphysis width	30.3; 31	29	27–38			
Its diameter	42; 41	39	32–46			
Phalanx 3 Length along upper edge	71.3; 73.7	78.3; 73	$n = 4$ 54.8–76.5		80	
Height	51; 49.3	47; 47.7	36–47			
Length along lower surface	75.5; 83.4	81.7; 84	70–82.5			

Table 5. Skeleton proportions in *Megaloceros giganteus* (Blum.)

Measurements, mm/proportions, %	Dzhambul, POIKM, no. KP 7191	Sapozhok PIN, no. 337	Kamyshlov SM/9925 (Pavlowa, 1908)
Basal skull length	465	650?	530
Vertebral column length without tail	2300	2320	
Skull length, % of vertebral column length	20.2	28.0?	
Length of vertebral column regions, % of total vertebral column length**:			
cervical	33.0(76)	25.9(60)?	
thoracic	37.6(86.5)		
lumbar	20.0(46)		
sacral	9.1(21)		
Forelimb length, % of vertebral column length	78.5		
Hind limb length, % of vertebral column length	68.3		
Length of free forelimb (without scapula), % of hind limb length	85.4		95.7
Length of neural spine of thoracic vertebra 2, % of vertebral column length	16.5		
Length of limb regions (without phalanges), in mm:			
scapula	465	470	–
humerus	355	380	400
radius	380	–	410
metacarpal	335	330	330
femur	460	480	530
tibia	470	470	350
metatarsal	375	360	360
Length of forelimb regions, in % of limb length:			
scapula	25.8*		without scapula
humerus	19.7(26.5)		29.8
radius	21.1(28.4)		28.3
metacarpal	18.6(25.0)		22.8
digit	10.8(13.4)		13.1
Pelvic length, in % of vertebral column length	21.7	23.3	
Length of hind limb regions, in % of limb length:			
femur	29.3	30.8	35.0
tibia	29.9	30.1	23.1
metatarsal	23.9	23.1	23.8
digit	13.8	11.0	10.2
Width of limb bone diaphyses, in % of length of these bones:			
scapula (greatest width)	58.1	57.4	—
humerus	13.7		13.95
metacarpal	13.4		12.5
femur	10.0		9.5
metatarsal	10.0		10.7
Width of distal epiphyses of limb bones, in % of length of these bones:			
humerus	27.2	25.0	20.9
radius	23.2		24.4
metacarpal	21.5		21.2
femur	27.3		28.1
tibia	18.1		25.7
metatarsal	19.1	21.4	16.7
Pelvic width, in % of its length:			
at wings	91.6		
at articulations	24.0		
at ischiadic projections	42.0		

* The relative length of limb regions without taking into account the scapula are shown in parenthesis.
** Absolute length measurements of vertebral column regions (cm) are shown in parenthesis.

locomotor features are reflected in the vertebral column structure. The body weight also has a great effect on the skeleton structure.

In the skeletons from Dzhambul, Kamyshlov, and Sapozhok, I calculated the ratios between the limb regions and the length of the skull and vertebral column and between individual limb bones and limb length; general comparison of these skeletons is provided below. The mounted skeleton from Dzhambul is 182 cm tall at the withers and 170 cm tall at the sacrum; at the upper edge of the scapula, the forelimb is 165 cm long; free forelimb (up to the breast) is 106 cm long. The head in the upper position is 250 cm above the ground (at the upper orbital rim); in the skeleton from Sapozhok, this measurement is 270 cm (Pavlowa, 1928, 1929). It should be noted that the skeleton from Kamyshlov is larger, particularly in regard to the proximal regions of limbs. Bone measurements of the skeleton from Dzhambul are close to that of deer from Sapozhok (Pavlowa, 1908, 1929). Table 5 shows the main skeleton proportions. The hind limbs of the giant deer from Dzhambul are much longer than the forelimbs (without taking into account the scapula). The ratio of the sum of the humerus, radius, and metacarpal lengths to the sum of the femur, tibia, and metatarsal lengths (length index of the forelimb after Vislobokova, 1990) is 0.82 in the deer from Dzhambul, that is, less than the data provided by Vislobokova (0.85) and the same index calculated by me for the skeleton from France, 0.84 (Croitor et al., 2006, table IX), and from Kamyshlov, 0.92 (in Table 5, this index is calculated taking into account small carpals, tarsals, and phalanges). The forelimb length correlates with the neck length. In opinion of Vislobokova, this depends on the feeding mode, forelimb length, and head weight. In *Megaloceros giganteus giganteus* from Dzhambul, the neck length is 33% of the total vertebral column length, that is, much greater than in elks (28–29% after Vislobokova, 1990), which feed on taller plants. At the same time, the forelimb length is approximately equal in the two species and the skull weight (because of antlers) in the giant deer is greater than in the elk. Consequently, the major factor of neck lengthening is the feeding mode; the giant deer fed mostly on grasses, consumption of which requires a low position of the head, while elks feed mostly on bush and tree sprouts, which do not require a low position of the head. The neck length of the skeleton from Sapozhok (60 cm) reported by Pavlowa (1929) is rather doubtful; the same concerns the skull length of 65 cm according to her data (in Table 5, these measurements are marked by ?). The wither of the giant deer is well developed; the neural spines of the first thoracic vertebrae are directed upwards at an angle of 60°, providing the optimum muscular efforts for vertical movements of the neck and maintenance of a heavy head in both upper position during locomotion and lower position during grazing. In the skeleton from Dzhambul, the longest neural spines are in thoracic vertebrae 2 and 3 [the same was indicated by Vislobokova (1990)], whereas in the skeleton from Kamyshlov, the longest neural spine is in vertebra 5 (Pavlowa, 1908).

The relative length of the metacarpal, or the metapodial index (the length ratio of the metacarpal and metatarsal mc/mt), in the deer from Dzhambul is 89.3%, that is, somewhat lower than in the specimens from Kamyshlov and Sapozhok (91.7%) (Fig. 6). This difference possibly results from a somewhat greater load on the forelimbs in the specimen from Dzhambul in connection with its larger antlers. Nevertheless, this index, along with the ratio of the upper limb regions (h/f = 77.2–81.1%), are most stable for these skeletons. A similar metapodial index (mc/mt = 91%) is calculated by me for *Megaloceros verticornis* (Dawkins, 1868) from Bilshausen (Germany: Pfeiffer, 2002). The proximal region of the hind limb (femur) is relatively longer than the distal region (metatarsus), particularly in the specimen from Kamyshlov. In the last, the relative femoral length is greater than that of the tibia and metatarsals by almost 12% (the absolute difference is 17–18 cm). In this connection, in the deer from Kamyshlov, the relative and absolute tibial length is close to that of the metatarsal rather than femur, as in the specimens from Dzhambul, Sapozhok, and Western Europe. In these deer, the hind limb proportions are generally similar to each other, as is seen from the curves of the ratios of the limb regions (Figs. 6, 7). In the forelimb, the lengths of particular regions are more regular. There are minor differences in the ratio of the relative (and absolute) length of the humerus and radius between the skeletons from Dzhambul and Kamyshlov; in the first, the relative length of the radius is greater than that of the humerus; in the second, the ratio is inverse. The skeleton from Kamyshlov shows significant deviations in the relative size of distal regions of some bones; in the humerus and metatarsal, they are small and, in the tibiae, the distal epiphysis is massive.

The phalanges of forelimbs of giant deer are more massive than hind limb phalanges, according to the greater load on the forelimbs.

CONCLUSIONS

Megaloceros giganteus existed from the beginning of the Middle Neopleistocene to the beginning of the Holocene. During this time, several climatic inversions accompanied primarily by changes in humidity and temperature occurred in northern Eurasia. The geographic range of the giant deer covered a vast area, with varying physiographic conditions. These circumstances apparently had an effect on morphological features of the giant deer in time and space. To date, certain morphological characters of the skull and antlers of the giant deer of different geological age that allow reliable division into two subspecies, Middle Neopleistocene *Megaloceros giganteus ruffi* and Late

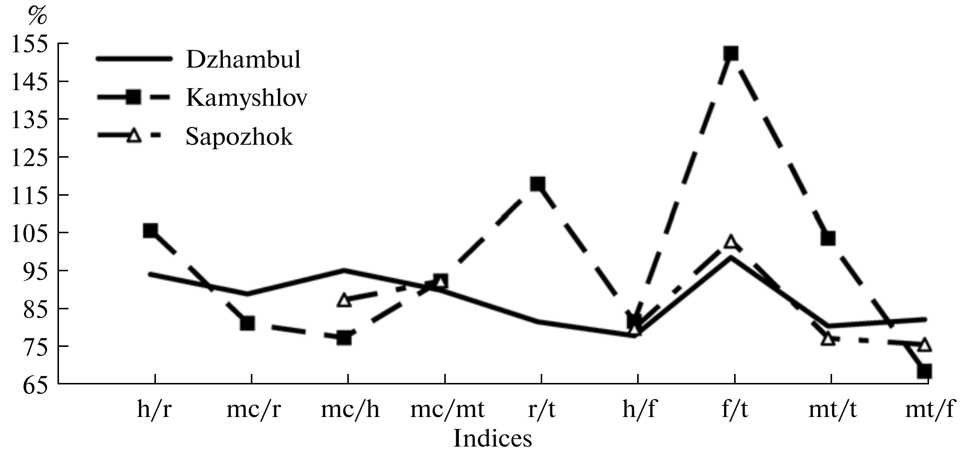


Fig. 6. Comparison of relative lengths of limb bones of *Megaloceros giganteus* (Blum.) from Dzhambul, Kamyshlov, and Sapozhok.

Neopleistocene *Megaloceros g. giganteus*, have been recognized (Shcheglova, 1958; Shpansky, 2011). These characters include the widely laterally open antlers in *M. g. giganteus* and the dorsally curved distal margins of palmations with tines in *M. g. ruffi*; in the skulls, measurements 1, 6, 7, 12, 16, 17, 19, 21, 22, and 26 and indices 2, 4, 12a, 16, 17a, 18a, 19a, and 20a reliably distinguish the two subspecies (Table 1). The skull indices reported by Vislobokova (1990) probably include the data on both subspecies, since most of them are close to the mean values. The establishment of similar distinctions in the lower jaw is complicated because of a lack of well-preserved lower jaws with precise geological dating, in the ideal case connected with diagnostic skulls. Nevertheless, describing lower jaws from Ukraine, Svistun (1968, table 18) indicated that the dental row of *M. g. ruffi* is 167–182 mm long (on average 174.5 mm) and, in *M. g. giganteus*, it is 164–170 mm long (on average 166.5 mm). He also marked the relative elongation of the premolar row in *M. g. giganteus* to 65.6% versus 62.4% in *M. g. ruffi*. For abundant postcranial remains, it is difficult to identify subspecies, since this requires complete and well-preserved skeletons or, what is still better, serial material from different geographical points of the geographical range, as, for example, in the case of mammoths (varying in individual age and sex).

At present, the giant deer skeleton from the Dzhambul locality is most complete and best preserved among the specimens described from Russia and Kazakhstan. The skeleton in question is assigned to the Late Neopleistocene subspecies *Megaloceros giganteus giganteus* based on the antler shape and structural features of the skull. This is evident from its widely spaced antlers, short skull with a long facial region, and short dental row.

In the evolutionary aspect, the most indicative characters of *Megaloceros giganteus* are changes in the absolute and relative lengths of the dental row and facial skull region. In *M. g. giganteus*, against a background of a significant decrease in length of the skull and dental row, the facial region is elongated. These changes are probably caused by changes in physiographic conditions. *M. g. ruffi* of the Tobolsk Interglacial probably inhabited forest–steppe and riverain meadows, feeding on herbs and branches; tearing and treatment of this food were facilitated by the short facial region and elongated dental row. In the Late Neopleistocene, the climate was much arider and open landscapes expanded; therefore, dwelling of the giant deer in tundra–steppe was connected with feeding on coarser herbs. The treatment of this forage required great muscular efforts [hence, the facial region increased in height (Table 1: measurement and index 12), the lower jaw lever and dental row became shorter (Table 1: 19)]. The elongation of the diastema (Table 1: 17) was probably compensatory (measurements 3, 15, 18 are identical in both subspecies) to

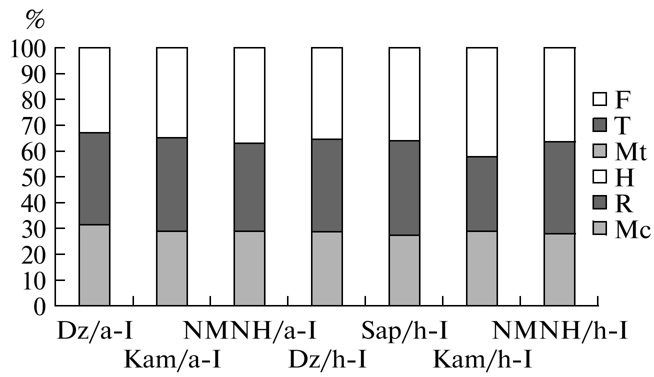
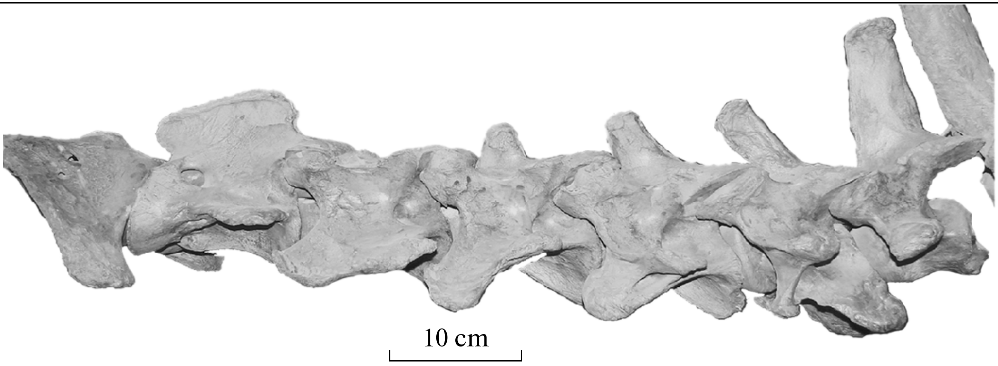


Fig. 7. Proportions of the main limbs regions in *Megaloceros giganteus* (Blum.). Designations: (*Dz*) Dzhambul; (*Kam*) Kamyshlov; (*Sap*) Sapozhok; (*NMNH*) National Museum of Natural History, Paris (Croitor et al., 2006); (*a-l*) forelimbs and (*h-l*) hind limbs.

Plate 15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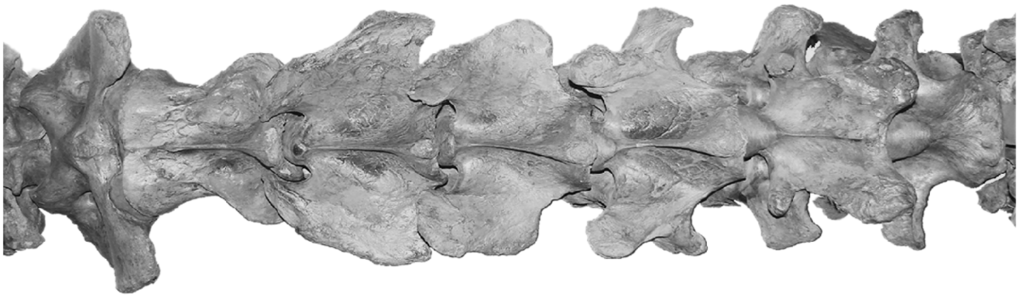
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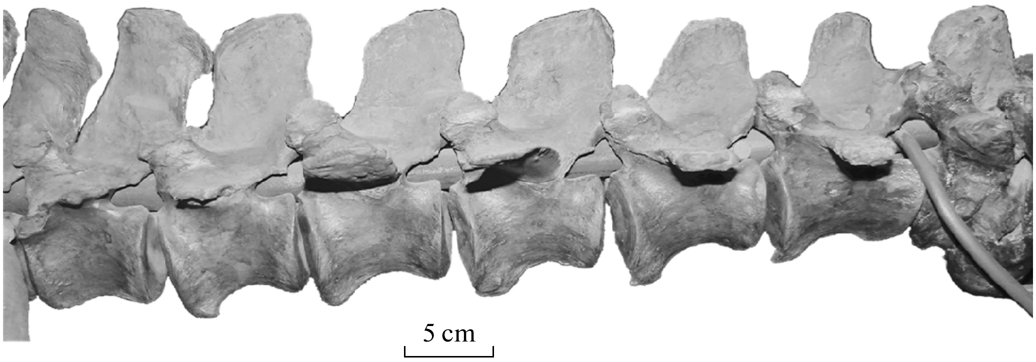
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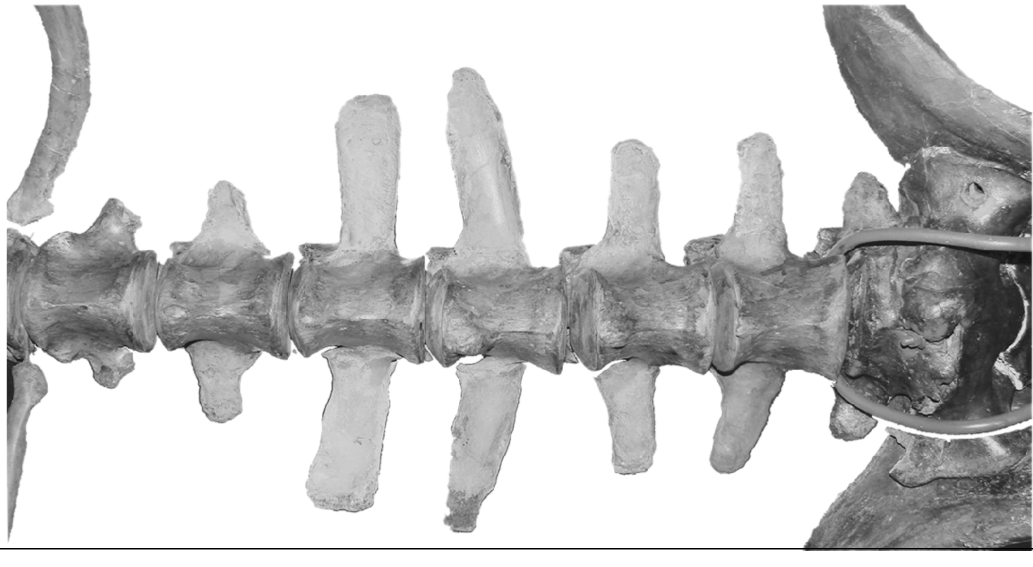
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Explanation of Plate 15

Figs. 1 and 2. *Megaloceros giganteus giganteus* (Blumenbach, 1803), specimen POIKM, no. KP 7191; Kazakhstan, Pavlodar Region, Dzhambul locality; Upper Neopleistocene, Karginian Horizon: (1) cervical vertebrae: (1a) lateral and (1b) ventral views; (2) lumbar vertebrae: (2a) lateral and (2b) ventral views.

retain a high position of orbits, since feeding on herbs means a low position of the head. Similar adaptive changes, but in a reverse sequence, are observed in the lower jaw of Late Neopleistocene and Holocene *Alces alces* L. of Western Siberia (Shpansky, 2001). The above distinctions of giant deer skulls are stable characters, at least in regard to the material from Western Siberia, and apparently correspond to the subspecies level. Comparative analysis involving materials from other regions requires well-preserved and stratigraphically characterized skulls of *Megaloceros giganteus* and the use of the same system of measurements and indices. Lister (1994) performed a thorough morphological analysis of giant deer antlers from various European localities, which has shown the absence of characters distinctly dividing noncontemporaneous specimens and specimens from different regions. The same concerns the earlier species *Megaloceros verticornis*, which dwelt in Europe in the first part of the Ionian (700–400 ka). Rather abundant specimens from Germany usually have poorly preserved skulls (Kahlke, 1965; Pfeiffer, 2002), although antlers of this deer clearly differ from antlers of *M. giganteus.* Pfeiffer (2002) performed comparative and cladistic analyses of the giant deer and other deer species based on 122 characters of the postcranial skeleton and showed the affinity between *M. verticornis* and *M. giganteus* and monophyletic origin of the genus.

In the present study, the skeleton proportions of three giant deer skeletons from localities of Western Siberia, the Urals, and Eastern Europe (from Dzhambul, Kamyshlov, and Sapozhok) are calculated for the first time. Comparison of these specimens with each other is somewhat difficult in connection with differences in geological age. The differences in proportions of the limb regions and bones of distal limb regions (the great massiveness of proximal regions and small size of the distal epiphysis of metapodials) and in absolute measurements suggest that these animals could have dwelt under somewhat different conditions. The Holocene deer from Kamyshlov (Sverdlovsk Region) could have had a rapider locomotion and was adapted for a harder ground, since it had long limbs and relatively slender distal limb regions. The same concerns individual limb bones of the giant deer from the Late Karginian Krasnyi Yar locality (Tomsk Region); they are rather long, with light distal epiphyses. In the deer from Dzhambul, the body is more compact, the trunk is shorter, and the limbs are relatively shorter, with large widely spaced hooves (Pl. 14, fig. 5). This suggests that its habitats had a more humid substrate, probably in humid riverain lowlands of lakes and floodplains. It is more difficult to reconstruct habitats for the skeleton from Sapozhok, the geological age of which is uncertain. In this specimen, the forelimb is not preserved, although the hind limb proportions are very similar to that of the giant deer from Dzhambul. In general, it is possible to assume that the deer from Kamyshlov was more specialized for inhabiting open landscapes, which was probably connected with dwelling in the Holocene under conditions of a restricted refuge.

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